Evaluation of *Ostrinia nubilalis* (Lepidoptera: Crambidae) Neonate Preferences for Corn and Weeds in Corn

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ABSTRACT Choice tests were conducted to determine feeding preferences of European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae), neonates for 15 species of plants. Percentage of neonates accepting (found on) each leaf disc after 24 h was measured using choice tests. Initially, nine species of plants were evaluated. The following year, 10 plant species were evaluated during *O. nubilalis* first generation and 11 species during the second generation. Pennsylvania smartweed, *Polygonum pennsylvanicum* (L.), had the highest percentage of neonates accepting leaf discs in both years. Other plants with high acceptance rates included swamp smartweed, *Polygonum amphibium* L.; velvetleaf, *Abutilon theophrasti* Medicus; cocklebur, *Xanthium strumarium* L.; and yellow foxtail, *Setaria glauca* (L.). Corn, *Zea mays* L., consistently had low percentages of neonates accepting leaf discs along with common waterhemp, *Amaranthus rudis* Sauer. Implications these results may have on *O. nubilalis* host plant selection in central Iowa's corn dominated landscape are considered.

KEY WORDS European corn borer, alternate hosts, feeding preference

European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae), is a serious pest of corn, *Zea mays* L., causing an estimated $1–2 billion in damage and control costs annually (Russnogle 1997, Hyde et al. 2001). European corn borer has a wide host range, infesting other grass species such as broomcorn, *Holcus sorghum* L., and proso millet, *Panicum miliaceum* (L.), and weed species such as pigweed, *Amaranthus retroflexus* L., cocklebur, *Xanthium strumarium* L., and Pennsylvania smartweed, *Polygonum pennsylvanicum* (L.) (Hodgson 1928). Host selection is influenced primarily by moth oviposition, but neonate ballooning and larval movement also are important (Ross and Ostlie 1990, Davis and Onstad 2000). Learning about feeding preferences of *O. nubilalis* neonates for different plant hosts will help decipher complex plant–insect interactions in cornfields and may help predict the degree of *O. nubilalis* infestations in weedy and nonweedy fields.

Choice tests with plant tissues are a common method for evaluating insect feeding preferences (Barnes and Ratcliff 1967, Jackai 1991, Smith et al. 1994). Insects are placed in an arena equidistant from all tissues and allowed to move to a preferred plant tissue (Kennedy and Schaefers 1974, Smith et al. 1992, Smith et al. 1994). *O. nubilalis* larval choice tests have identified specific sugars and amino acids as potential feeding stimulants (Beck and Hanec 1958, Bartelt et al. 1990) and fiber content and phenolic fortification as potential feeding deterrents (Bergvinson et al. 1995). Studies with inbred and wild varieties of corn suggest *O. nubilalis* feeding deterrents vary with plant phenology (Guthrie et al. 1960, Guthrie 1989, Abel et al. 1995). However, no studies have evaluated *O. nubilalis* larval behavior on alternate hosts. In Iowa, availability and phenology of alternate hosts varies by *O. nubilalis* generation. Some weed species such as pale dock, *Rumex altissimus* Wood, are in the reproductive stage in June during the first *O. nubilalis* generation, whereas many other weed species (most of those tested in these studies) are in the reproductive stage at the end of July or later during the second *O. nubilalis* generation. Perhaps *O. nubilalis* larval responses to weed tissues will vary with plant phenology as observed in corn (Abel et al. 1995).

Understanding neonate host plant preferences will help decipher *O. nubilalis* interactions with corn and weeds in cornfields. Choice tests were used to evaluate relative preferences of *O. nubilalis* neonates for corn and a total of 14 other plant species in June, August, and September–October.

Materials and Methods

Laboratory choice tests were conducted in 1996 and 1997 to evaluate *O. nubilalis* neonate preference between 15 weed and agronomic crop species. These tests were conducted with plants collected on five fall dates in 1996, which corresponded with a partial third

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generation of *O. nubilalis* neonates, and on eight dates in 1997, which corresponded with the presence of first and second generation neonates.

September–October 1996. Nine species of plants were tested: cocklebur, corn (B73 × Mo17); fall panicum, *Panicum dichotomiflorum* Michaux.; German foxtail millet, *Setaria italica* (L.) Beauvois; giant foxtail, *Setari faberi* Herrmann.; Japanese millet, *Echinochloa frumentacea* Roxburgh; Pennsylvania smartweed; proso millet; and yellow foxtail, *Setaria glauca* (L.) Beauvois. Plants were collected on 15, 21, and 22 September and 5 and 8 October at the Iowa State Foundation Johnson Farm, Ames, IA. These dates correspond with a partial third generation of *O. nubilalis*, observed in Iowa. Leaf material was collected only from reproductive stage weeds and corn. Weed species were designated reproductive stage when seed heads were present. Harvested plants were placed on ice, transported to the laboratory, and processed for choice tests conducted the same day. Choice tests were replicated five times on each September date and seven times on each October date.

Choice tests were conducted in 100- by 15-mm polystyrene petri dishes (Fisher International Inc., Hampton, NH). Each petri dish, or arena, contained a Whatman 90-mm filter paper (Whatman, Maidstone, England) moistened with 750 μl of deionized water to prevent desiccation of larvae and leaves. Leaves from the middle third of test plants were cut into discs with a #10 (14-mm-diameter) brass-plated cork borer (#1601 AE, Boekel Inc., Featerville, PA). Four leaf discs, two from each of two plant species, were placed in arenas equidistant from the center ($\approx$45 mm). The location of each species was denoted by species-specific letters applied to petri dish bottoms with a permanent marker. One blackhead stage *O. nubilalis* egg mass ($\approx$20 eggs), obtained from a colony maintained at the USDA–ARS Corn Insects and Crop Genetics Research Unit, Ames, IA, was placed in the center of the filter paper. Petri dishes were sealed with ParafilmM (American National Can, Neenah, WI). Arenas were placed in a model I-35VL environmental chamber (Percival Scientific, Perry, IA) at 26°C, 80% humidity, and a photoperiod of 16:8 (L:D) h in a randomized complete block design. After 24 h, numbers of neonates found on and off leaf discs were recorded.

June 1997. Ten species of plants were evaluated in choice tests, including cocklebur, corn (B73 × Mo17), giant foxtail, Pennsylvania smartweed, and yellow foxtail as in choice tests conducted in September–October. The five additional species included brome grass, *Bromus inermis* Leyss; common waterhemp, *Amaranthus rudis* Sauer; pale dock; soybean, *Glycine max* (L.) Merrill; and velvetleaf, *Abutilon theophrasti* Medicus. Plants were collected at the Iowa State Foundation Burke Research Farm, Boone, IA, on 6, 12, 20, and 27 June, which correspond with the first generation of *O. nubilalis* in Iowa. Primarily vegetative leaf material was collected, which for the weed species meant no seed head present. Pale dock was the only exception owing to early emergence and senescence during the growing season. Choice tests were conducted as in September–October the previous year with five replications on each date.

August 1997. Eleven species of plants also were evaluated in choice tests, including: 10 species previously evaluated in June. Swamp smartweed, *Polygonum amphibium* L., was the only addition to choice tests conducted in August. Plants were collected at the Iowa State Foundation Burke Research Farm on 1, 8, 15, and 22 August, which correspond with the second generation of *O. nubilalis.* Only leaf material from reproductive-stage plants was used. Choice tests were conducted as described previously and replicated five times on each date.

Analyses. Arena comparisons and plant species were analyzed by a two-way analysis of variance (ANOVA) under an incomplete block design for each trial (PROC GLM, SAS Institute 1996). The comparisons were incomplete because same-plant comparisons were not conducted. Least-square means for the percentage of neonates observed on a species leaf disc were used to calculate overall plant acceptance means for each species. Least-square means also were calculated for September–October (1996), June (1997), and August (1997). These data were analyzed with a one-way ANOVA. Analyses were conducted across all months and separately for each month. Data were arcsine transformed when distributions were skewed. Acceptance means were separated using least significant difference (LSD) (STDERR = PDIFF, SAS Institute 1996) if the ANOVA was significant ($\alpha \leq 0.05$).

Neonate responses to leaf discs in cocklebur, common waterhemp, corn, giant foxtail, yellow foxtail, Pennsylvania smartweed, and velvetleaf arenas were further evaluated. The percentage of difference in responses between plant discs and nonselector percentages were evaluated for each paired plant comparison, where percentage of difference = [(neonates found on species 1) − (neonates found on species 2)]/(total neonates) × 100; and nonselector percentage = (neonates found off both species)/(total neonates) × 100 were calculated. Percentage of difference and nonselector percentages were analyzed with one-way ANOVA by month and across all months. Data were arcsine transformed when distributions were skewed. LSD tests were used to separate means if the ANOVA was significant (SAS Institute 1996).

Results

Acceptance Means. Neonate acceptance of leaf discs was significantly different among choice test months (F = 168.1; df = 2, 4,256; P < 0.0001). In September–October 1996 choice tests, acceptance means for six of eight species' leaf discs were significantly higher than that of corn (Fig. 1A). In June, leaf discs of eight species were accepted by significantly higher percentages of neonates than were corn leaf discs (Fig. 1B). Neonates accepted significantly higher percentages of Pennsylvania smartweed leaf discs than discs of any other plants; and neonates accepted significantly lower percentages of common water-

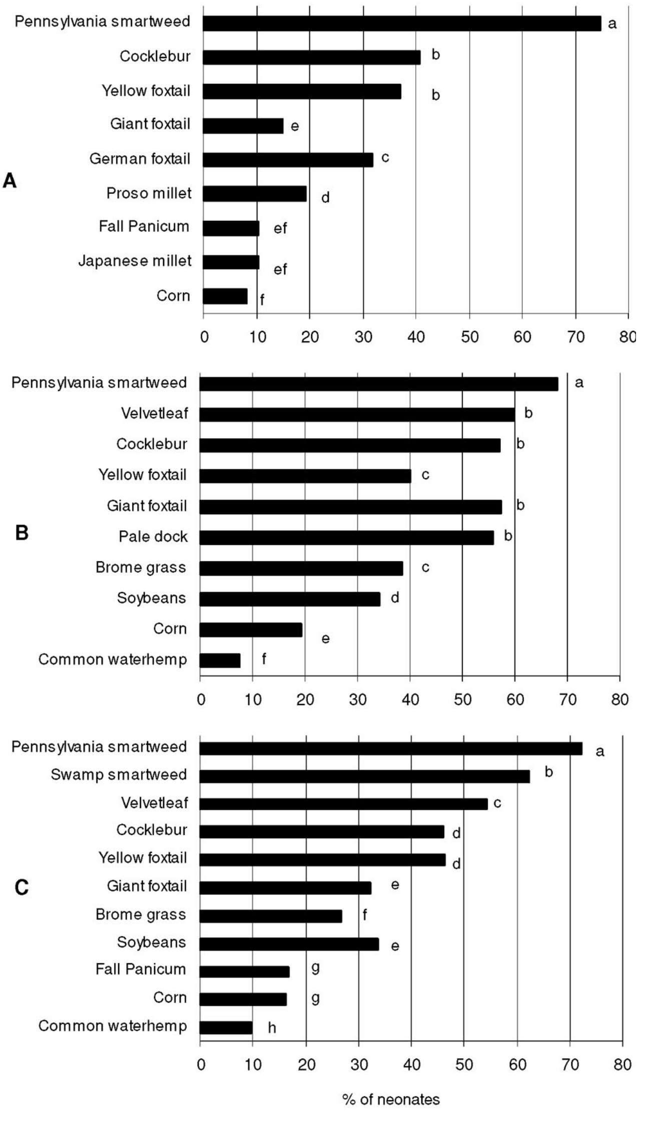

Fig. 1. Cumulative mean percentage of neonates accepting leaf discs of indicated species in choice tests. Means calculated from percentages of neonates accepting individual species leaf discs in all arenas. (A) September–October choice tests ($F = 136.5$; df = 8, 576; $P < 0.0001$). (B) June choice tests ($F = 380.8$; df = 9, 1,679; $P = 0.0001$). (C) August choice tests ($F = 263.4$; df = 10, 1,989; $P < 0.0001$). Bars marked with the same letter are not significantly different (ANOVA, $P \leq 0.05$; LSD, $\alpha = 0.05$).

hemp leaf discs than any other leaf discs (Fig. 1B). In August, significantly higher percentages of neonates accepted Pennsylvania smartweed leaf discs than any other plants (Fig. 1C). Significantly lower percentages of neonates accepted corn, common waterhemp, and fall panicum leaf discs compared with leaf discs from the other eight plants (Fig. 1C).

Corn and Weed Comparisons. These analyses focused on corn when it was paired with weeds commonly found in cornfields. Mean percentages of neonates selecting various leaf discs significantly differed among trials (month: $F = 18.5$.; df = 2, 563; $P < 0.0001$) and arenas ($F = 17.2$; df = 80, 4,256; $P < 0.0001$). In addition, significantly different percentages of neonates selected leaf discs in arenas comparing cocklebur, common waterhemp, giant foxtail, yellow foxtail, Pennsylvania smartweed, and velvetleaf with corn (Table 1). Nonselector percentage and percentage difference also were significantly different among arenas (Table 1).

September. Differences (percentages) in neonate leaf discs acceptance were significantly different in arenas comparing Pennsylvania smartweed, giant and yellow foxtails, and cocklebur with corn (Table 1). However, significantly smaller differences were observed in corn–cocklebur arenas than in corn–Pennsylvania smartweed and corn–yellow foxtail arenas. In addition, nonselector percentages were significantly

Table 1. September–October 1996 (partial third generation), June 1997 (first generation), and August 1997 (second generation) arena means ± SE for the percentage of neonates accepting when presented with a choice of two species (acceptance mean), the number of arenas evaluated (*n*), the percentage of neonates not found on any leaf discs (% nonselector), and the percentage of difference in acceptance between the paired species relative to the total number of neonates (% difference)

Mo	Plant 1	Mean	Plant 2	Mean	n	% difference[a]	% nonselector[b]
Sept.	Corn	7.4 ± 2.5	Giant foxtail	24.6 ± 5.5	14	78.7 ± 10.2ab	68.1 ± 5.8a
	Corn	4.6 ± 1.2	Yellow foxtail	61.9 ± 5.1	28	89.4 ± 9.5a	34.8 ± 5.4b
	Corn	12.6 ± 3.3	Cocklebur	45.1 ± 7.4	7	52.4 ± 13.0b	42.3 ± 5.4b
	Corn	0.4 ± 0.3	Pennsylvania smartweed	73.2 ± 4.7	28	99.0 ± 1.0a	26.4 ± 4.7b
June	Corn	51.1 ± 27.3	Common waterhemp	12.4 ± 11.5	20	68.9 ± 6.3b	34.6 ± 4.6a
	Corn	10.4 ± 9.9	Giant foxtail	79.0 ± 12.3	20	76.3 ± 4.9ab	10.4 ± 1.6b
	Corn	17.3 ± 18.7	Cocklebur	70.5 ± 22.5	20	67.2 ± 6.0b	12.3 ± 2.7b
	Corn	11.5 ± 11.0	Velvetleaf	72.7 ± 15.9	20	72.3 ± 5.7b	15.8 ± 2.9b
	Corn	4.4 ± 4.3	Pennsylvania smartweed	84.6 ± 5.1	20	90.1 ± 2.1a	10.8 ± 1.6b
Aug.	Corn	32.6 ± 26.2	Common waterhemp	14.6 ± 15.1	20	49.1 ± 7.9c	52.8 ± 4.6a
	Corn	18.1 ± 15.7	Giant foxtail	50.2 ± 22.5	20	58.8 ± 7.4bc	31.7 ± 3.9b
	Corn	14.3 ± 9.7	Cocklebur	61.0 ± 26.5	20	62.2 ± 6.2bc	24.7 ± 4.8bc
	Corn	12.7 ± 12.4	Velvetleaf	70.7 ± 17.7	20	50.7 ± 6.1ab	16.6 ± 2.7cd
	Corn	7.5 ± 10.6	Pennsylvania smartweed	80.8 ± 13.6	20	84.4 ± 4.9a	10.7 ± 1.8d

Mean, acceptance means.

Means within column and month followed by the same letter are not significantly different ($P > 0.05$).

Arena acceptance means were significantly different (month: $F = 18.5$; df = 2, 563; $P < 0.0001$; arena: $F = 9.0$; df = 5, 563; $P < 0.0001$). September–October 1996, partial third generation, arena acceptance means: $F = 12.5$; df = 8, 237; $P < 0.0001$; June 1997, first generation, arena acceptance means: $F = 31.9$; df = 16, 679; $P < 0.0001$; and August 1997, arena acceptance means: $F = 20.1$; df = 16, 687; $P < 0.0001$. Nonselector percentages (September–October: $F = 10.0$; df = 29, 288; $P < 0.0001$; June: $F = 5.5$; df = 44, 839; $P < 0.0001$; August: $F = 8.5$; df = 54, 992; $P < 0.0001$) and percentage difference (September–October: $F = 3.5$; df = 29, 288; $P < 0.0001$; June: $F = 13.5$; df = 44, 839; $P < 0.0001$; August: $F = 5.6$; df = 54, 992; $P < 0.0001$) among arenas also were significantly different.

Percentage of nonselectors among arenas comparing corn leaf discs with leaf discs from specific weed species leaf discs were significantly different (September–October arena nonselector percentage means: $F = 8.3$; df = 3, 76; $P < 0.0001$; June arena nonselector percentage means: $F = 9.6$; df = 4, 99; $P < 0.0001$; and August arena nonselector percentage means: $F = 16.7$; df = 4, 104; $P < 0.0001$). Additionally, percentage difference between leaf discs among specific arenas also were significantly different (September–October arena percentage difference means: $F = 3.7$; df = 3, 76; $P = 0.02$; June arena percentage difference means: $F = 3.1$; df = 4, 99; $P = 0.02$; and August arena percentage difference means: $F = 3.9$; df = 4, 104; $P = 0.01$).

[a] Arena percentage difference means marked with the same letter are not significantly different (ANOVA, $P \leq 0.05$; LSD, $\alpha = 0.05$).

[b] Nonselector percentage means marked with the same letter are not significantly different (ANOVA, $P \leq 0.05$; LSD, $\alpha = 0.05$).

higher in corn–giant foxtail arenas than all other arenas (Table 1).

June. Differences (percentages) in leaf disc acceptance differed significantly in arenas comparing Pennsylvania smartweed, velvetleaf, giant foxtail, and cocklebur with corn (Table 1). Corn–Pennsylvania smartweed arenas had significantly larger differences in leaf disc acceptance than all other arenas, except corn–giant foxtail arenas. Nonselector percentages were significantly higher in corn–common waterhemp arenas than the other arena types (Table 1).

August. As in June, differences (percentages) in leaf disc acceptance were significantly different in arenas comparing test species (Table 1). Corn–common waterhemp arenas had significantly smaller percentage differences than corn–Pennsylvania smartweed and corn–velvetleaf arenas. In addition, corn–common waterhemp arenas had significantly higher nonselector percentages than all other arenas (Table 1). Nonselector percentages were significantly lower in corn–Pennsylvania smartweed arenas than other test arenas, except corn–velvetleaf.

Weed Comparisons. These analyses focused on comparing weeds commonly found in cornfields. Mean percentages of neonates selecting various leaf discs significantly differed among trials (month: $F = 11.0$; df = 2, 801; $P < 0.0001$) and arenas ($F = 6.2$; df = 11, 801; $P < 0.0001$). Additionally, significantly different percentages of neonates selected leaf discs in arenas comparing cocklebur, common waterhemp, giant foxtail, yellow foxtail, Pennsylvania smartweed, and velvetleaf with one another (Table 2). Nonselector percentages and percentage difference also were significantly different among arenas (Table 2).

September–October. Differences (percentages) in neonate leaf disc acceptance were significantly different in arenas comparing Pennsylvania smartweed, giant and yellow foxtails, and cocklebur (Table 2). Pennsylvania smartweed–giant foxtail arenas had significantly larger differences than other test arenas, with the exception of cocklebur–giant foxtail arenas. Nonselector percentages were significantly higher in cocklebur–giant foxtail, cocklebur–yellow foxtail, and giant–yellow foxtail arenas than in other arenas.

June. Arena differences (percentages) in leaf disc acceptance were significantly different in arenas comparing Pennsylvania smartweed, velvetleaf, giant foxtail, and cocklebur (Table 2). Differences in leaf disc acceptance were significantly larger in giant foxtail–common waterhemp arenas than other test arenas, except in Pennsylvania smartweed–common waterhemp and cocklebur–common waterhemp arenas. In general, nonselector percentages were significantly lower in arenas containing Pennsylvania smartweed except for Pennsylvania smartweed–common waterhemp arenas (Table 2). Nonselector percentages were higher in arenas containing common waterhemp.

Table 2. September–October 1996 (partial third generation), June 1997 (first generation), and August 1997 (second generation) arena means ± SE for the percentage of neonates accepting when presented with a choice of two species (acceptance mean), the number of arenas evaluated (*n*), the percentage of neonates not found on any leaf discs (% nonselector), and the percentage of difference in acceptance between the paired species relative to the total number of neonates (% difference)

Mo	Plant 1	Mean	Plant 2	Mean	*n*	% difference[a]	% nonselector[b]
Sept.	Pennsylvania smartweed	89.0 ± 3.6	Giant foxtail	1.1 ± 0.7	7	97.3 ± 1.8a	9.8 ± 3.2b
	Pennsylvania smartweed	68.1 ± 4.5	Yellow foxtail	15.7 ± 3.9	14	65.6 ± 8.0b	16.2 ± 5.2b
	Pennsylvania smartweed	75.7 ± 4.1	Cocklebur	15.1 ± 4.8	7	68.0 ± 9.8b	9.2 ± 3.5b
	Cocklebur	45.3 ± 5.4	Giant foxtail	5.7 ± 2.4	7	76.4 ± 11.3ab	48.9 ± 4.7a
	Cocklebur	38.9 ± 8.8	Yellow foxtail	10.0 ± 2.0	7	53.3 ± 10.2b	51.2 ± 8.4a
	Yellow foxtail	23.9 ± 17.6	Giant foxtail	5.3 ± 5.8	14	52.0 ± 13.3b	70.0 ± 9.3a
June	Pennsylvania smartweed	82.0 ± 11.5	Common waterhemp	4.3 ± 7.0	20	88.0 ± 4.1ab	12.9 ± 1.8abc
	Pennsylvania smartweed	65.5 ± 16.8	Giant foxtail	29.9 ± 15.8	20	43.6 ± 4.6c	4.5 ± 1.0f
	Pennsylvania smartweed	53.1 ± 15.4	Cocklebur	40.0 ± 15.3	20	21.9 ± 4.9d	9.2 ± 2.5def
	Pennsylvania smartweed	49.6 ± 13.8	Velvetleaf	44.8 ± 14.5	20	20.5 ± 4.7d	5.7 ± 1.4ef
	Velvetleaf	72.5 ± 15.9	Common waterhemp	10.1 ± 10.0	15	75.3 ± 6.1b	17.4 ± 2.5a
	Velvetleaf	54.9 ± 13.6	Giant foxtail	37.6 ± 12.0	20	24.3 ± 4.8d	7.5 ± 1.2cdef
	Velvetleaf	49.9 ± 13.0	Cocklebur	39.4 ± 11.7	20	21.6 ± 3.6d	9.1 ± 2.1bcde
	Cocklebur	77.9 ± 16.5	Common waterhemp	7.6 ± 8.4	20	83.0 ± 4.6ab	15.2 ± 3.2ab
	Cocklebur	42.0 ± 17.1	Giant foxtail	47.4 ± 17.8	20	29.8 ± 5.6d	10.5 ± 1.4bcd
	Giant foxtail	83.8 ± 9.0	Common waterhemp	4.1 ± 4.8	20	90.5 ± 2.6a	12.2 ± 1.4abcd
Aug.	Pennsylvania smartweed	86.2 ± 12.7	Common waterhemp	2.5 ± 4.1	20	93.9 ± 2.4a	11.3 ± 2.3d
	Pennsylvania smartweed	80.8 ± 13.6	Giant foxtail	9.7 ± 10.5	20	78.6 ± 5.1ab	9.5 ± 2.1d
	Pennsylvania smartweed	68.4 ± 19.5	Cocklebur	23.7 ± 18.0	20	53.2 ± 6.9e	8.0 ± 1.9d
	Pennsylvania smartweed	62.4 ± 18.7	Velvetleaf	28.3 ± 13.6	20	40.6 ± 5.9e	9.3 ± 2.3d
	Velvetleaf	66.9 ± 18.8	Common waterhemp	5.9 ± 7.8	20	85.4 ± 4.3ab	27.2 ± 4.6ab
	Velvetleaf	60.1 ± 17.1	Giant foxtail	17.9 ± 11.7	20	55.2 ± 7.5cde	22.2 ± 2.2b
	Velvetleaf	50.7 ± 21.6	Cocklebur	34.8 ± 25.4	20	50.7 ± 6.1e	13.9 ± 3.1cd
	Cocklebur	64.4 ± 23.7	Common waterhemp	9.4 ± 8.6	20	69.7 ± 6.4bcd	15.2 ± 3.2ab
	Cocklebur	44.7 ± 26.8	Giant foxtail	36.0 ± 25.8	20	53.6 ± 6.1de	19.4 ± 3.2bc
	Giant foxtail	56.8 ± 18.2	Common waterhemp	8.8 ± 7.4	20	71.3 ± 5.9bc	34.4 ± 3.6a

Mean, acceptance means.

Means within column and month followed by the same letter are not significantly different ($P > 0.05$).

Arena acceptance means were significantly different (month: $F = 11.0$; df = 2, 801; $P < 0.0001$; arena: $F = 6.2$; df = 11, 801; $P < 0.0001$). September–October 1996, partial third generation, arena acceptance means: $F = 12.5$; df = 8, 237; $P < 0.0001$; June 1997, first generation, arena acceptance means: $F = 31.9$; df = 16, 679; $P < 0.0001$; and August 1997, arena acceptance means: $F = 20.1$; df = 16, 687; $P < 0.0001$. Nonselector percentages (September–October: $F = 10.0$; df = 29, 288; $P < 0.0001$; June: $F = 5.5$; df = 44, 839; $P < 0.0001$; August: $F = 8.5$; df = 54, 992; $P < 0.0001$) and percentage difference (September–October: $F = 3.5$; df = 29, 288; $P < 0.0001$; June: $F = 13.5$; df = 44, 839; $P < 0.0001$; August: $F = 5.6$; df = 54, 992; $P < 0.0001$) among arenas also were significantly different.

Percentage of nonselectors among specific arenas were significantly different (September–October arena nonselector percentage means: $F = 13.0$; df = 5, 47; $P < 0.0001$; June arena nonselector percentage means: $F = 5.1$; df = 9, 199; $P < 0.0001$; and August arena nonselector percentage means: $F = 8.6$; df = 9, 198; $P < 0.0001$). Additionally, percentage difference between leaf discs among specific arenas also were significantly different (September–October arena percentage difference means: $F = 2.6$; df = 5, 47; $P = 0.04$; June arena percentage difference means: $F = 43.0$; df = 9, 199; $P < 0.0001$; and August arena percentage difference means: $F = 8.6$; df = 9, 198; $P < 0.0001$).

[a] Arena percentage difference means marked with the same letter are not significantly different (ANOVA, $P \leq 0.05$; LSD, $\alpha = 0.05$).

[b] Nonselector percentage means marked with the same letter are not significantly different (ANOVA, $P \leq 0.05$; LSD, $\alpha = 0.05$).

August. Similar to June results, differences (percentages) in neonate leaf disc acceptance were significantly different among arenas (Table 2). Differences in leaf disc acceptance were significantly larger in Pennsylvania smartweed–common waterhemp than other test arenas, excluding Pennsylvania smartweed–giant foxtail and Velvetleaf–common waterhemp arenas. Nonselector percentages were significantly lower in arenas containing Pennsylvania smartweed than all other arenas, except in velvetleaf–cocklebur arenas (Table 2). In contrast, nonselector percentages were higher in arenas containing common waterhemp, except in Pennsylvania smartweed–common waterhemp arenas.

Discussion

Host preference of lepidopteran pests has been studied more extensively in later instars and adults than early instars (neonates and first instars). Often, later instars are chosen because conducting observational bioassays with them is less problematic than with smaller instars (Zalucki et al. 2002). These studies assume early and late instars behavior are similar (Stamp and Casey 1993, Bernays and Chapman 1994), which may not be the case (Zalucki et al. 2002). Many host preference studies with adult females suggest that females discriminately oviposit on suitable hosts (Courtney et al. 1989, Thompson and Pellmyr 1991). However, recent studies suggest female oviposition of some Lepidoptera is less discriminatory than assumed (Bernays and Chapman 1994) and is influenced by several factors (e.g., landscape and plant availability) (Foster and Howard 1999, Zalucki et al. 2002). Thus, understanding neonate host preference has become more important.

Hodgson (1928) evaluated *O. nubilalis* (larvae and adult) host preference and found that oviposition and larval infestations occur more in corn than in weed species closely associated with corn. Previous studies reported significant *O. nubilalis* infestations in weeds (Neiswander and Huber 1927, Huber et al. 1928). In this study, relatively low percentages of neonates accepted corn leaf discs when given a choice of corn or commonly found weed species. Pennsylvania smartweed, velvetleaf, and cocklebur, documented hosts of *O. nubilalis* (Caffrey and Worthley 1927, Hodgson 1928), were accepted by neonates at significantly higher percentages than corn. This finding suggests that these plants could be important *O. nubilalis* hosts. In particular, the highest percentages of neonates consistently accepted Pennsylvania smartweed, which has been documented to support *O. nubilalis* development in 60% of infested stems (Hodgson 1928).

In this study, plant phenology significantly influenced neonate host preference, which agrees with a report by Hodgson (1928). Highly preferred plants in June trials were selected at lower percentages later in the growing season (August and September), suggesting that preference is influenced by plant senescence and host suitability changes during the growing season. Changes in neonate acceptance based on plant phenology and high neonate acceptance of weed species suggest *O. nubilalis* is an opportunistic herbivore. Weed comparisons suggest the Pennsylvania smartweed, cocklebur, and velvetleaf, but not common waterhemp, are particularly attractive to larvae. Other lepidopterans (e.g., *Heliothis* spp.) have exhibited opportunistic behavior owing to plant availability becoming pests on a variety of hosts (Bernays and Chapman 1994).

Large numbers of European corn borer larvae are associated with weeds in Iowa cornfields (R.L.H., unpublished data). Nagy (1976) also reported no ovipositional preference for corn compared with cultivated hemp, *Cannabis sativa* L., or common mugwort, *Artemisia vulgaris* L. This nonpreference may explain why *O. nubilalis* females oviposit on corn, which dominates the landscape in Iowa. European corn borers may prefer weed species related to Pennsylvania smartweed, velvetleaf, or cocklebur, but perhaps females oviposit on corn because it is the predominate species in the area. Alternatively, there may have been a host preference shift. However, questions remain regarding larval fitness when reared on weeds as opposed to corn in the midwestern states. Losey et al. (2001) reported low larval survival on weeds compared with field corn in the northeastern United States. If larval fitness is affected, concomitant selection on adult oviposition preference may be low. Additionally, low neonate acceptance in arenas containing common waterhemp suggests that repellent compounds may be present. Further investigation is required to decipher *O. nubilalis* interactions with weeds in the field.

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